

## HAS MARINE ANTARCTIC ECOSYSTEM CHANGED?— A TENTATIVE COMPARISON OF PRESENT AND PAST MACROZOOPLANKTON ABUNDANCES

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**Abstract:** The N70V net, a small silk ring net of 70 cm in diameter which was originally designed by the Discovery Committee for collecting macrozooplankton in the Antarctic Ocean was reconstructed, and the collection with this net was made after the similar sampling procedures to the Discovery Investigations during the BIOMASS SIBEX I (1983-84) investigation. The abundances of total zooplankton biomass and of four major herbivorous copepod species were compared with the corresponding data of the Discovery Investigations 50-60 years ago when the marine Antarctic ecosystem was almost in its initial state. The total zooplankton biomass at present is well within the variation of possible sampling bias of the Discovery result, and is considered to have been almost unchanged during the past several decades. On the other hand, the abundance of three of four major herbivorous copepods, *Calanus propinquus*, *Calanoides acutus*, and *Rhincalanus gigas*, is remarkably poorer with the magnitudes of 1/10 to 1/100 in more than 70% of average figures of the present study than that reported in the Discovery Investigations. These results suggest that there occurred possible changes in the abundance and the relative compositions of macrozooplankton community of the Antarctic Ocean. Especially, a change in the abundance of major herbivorous copepods is noteworthy, since it must have resulted from an increase in the stock size of unconsumed krill, *Euphausia superba*, which perhaps caused some changes in the feeding conditions among other herbivorous animals.

### 1. Introduction

Studies on the current status of Antarctic krill stocks along with their biological and ecological aspects are the major topics of the BIOMASS program (SCAR and SCOR, 1977). It was, however, also hoped to know possible long-term changes in the marine Antarctic ecosystem in relation to long-lasting large scale exploitations of baleen whales that are the principal consumer of the Antarctic krill, *Euphausia superba*, a key species of herbivorous macrozooplankton in the Antarctic marine ecosystem.

The biomass of southern baleen whales that feed largely on *E. superba* is estimated as high as 43.09 million t (ca. 2.58 g/m<sup>2</sup>) in the early 1900's, while it is 6.62 million t (ca. 0.399 g/m<sup>2</sup>) at present (LAWS, 1977). This estimation leads to a consideration that there must exist a surplus of krill, and the estimated amount of such krill stocks left unconsumed by whales is as much as 153 million t (ca. 4.2 g/m<sup>2</sup>). Examining the food habits and the stock size of baleen whales, OMURA (1973) concluded that some 100-200 million t of krill are left untouched by the whales in their feeding grounds.

These surplus of krill have been undoubtedly consumed by the whales in the early 1900's when the whole Antarctic marine ecosystem was in their initial state. After the development of whaling industry, a gradual increase in the stock size of unconsumed krill had begun, and this might have resulted to show a possible change in some prey-predator relationships in the Antarctic animal community. Actually, whales are reported to attain to sexual maturity at younger ages than before, and another evidence is a recent increase in population sizes of pinnipeds, especially fur seals, crabeater seals and seabirds (LAWS, 1977). All these are considered to be the phenomena in response to the increased availability of forage among the animals competing with baleen whales. Even though the summer biomass of seals and seabirds is estimated as 0.58 g/m<sup>2</sup> and 0.03 g/m<sup>2</sup>, respectively (LAWS, 1977), it is expected that there still exists an enormous amount of unconsumed krill.

*E. superba* is the well known herbivorous zooplankton and the increase in its stock size may affect the abundance of other zooplankters that share a similar and/or same plant food with *E. superba*.

The principal aim of this study is to compare the data on macrozooplankton abundances in the Southern Ocean at present and in the past, and is also to give rise to further discussions about a possible change in the lower trophic communities in the marine Antarctic ecosystem, since there is no reason to believe that such possible changes as observed in pinnipeds, whales and seabirds have occurred in larger predatory animals alone.

## 2. Materials and Methods

The R. V. HAKUHO MARU of the Ocean Research Institute, University of Tokyo participated in the BIOMASS SIBEX I investigations, and made a cruise KH-83-4 to the Southern Ocean between the Pacific and Indian Ocean sectors during November 21, 1983–February 22, 1984 (MURANO *et al.*, 1984). As one of the plankton sampling schemes during the investigations, I prepared two sets of the N70V plankton net used routinely in the Discovery Investigations for the capture of the medium and smaller sized macrozooplankton (KEMP *et al.*, 1929). Due to the limited availability of materials in constructing the net, the duplicated N70V net was slightly different in the mesh size of bolting silk cloth, as shown in Table 1. As HOPKINS (1971) compared zooplankton biomass from the Eltanin investigations with FOXTON's data, the comparison of the Antarctic zooplankton biomass is considered to be possible as far as some reasonable sampling gear is used for this purpose. The general construction of the net was dupli-

Table 1. Netting of the original and reconstructed N70V nets.

Part of net	Original	Reconstructed
Upper	1/4 inch coarse net	Nylon 210 <sup>D</sup> /15F/2
Front	0.569 mm (# 40)*	0.473 mm (# GG40)**
Behind	0.239 mm (# 74)*	0.222 mm (# GG72)**

\* Messers Staniar's "Quadruple Extra Heavy Quality Double Twist Swiss Silk".

\*\* Nippon Bolting Cloth (NBC) silk cloth.

Table 2. Sampling data of the N70V net tows during the BIOMASS SIBEX I cruise of the R.V. HAKUHO MARU.

Station	Date	Location	Sea region	Water column fished (m)*	Sampling condition (Day/Night)
1	Dec. 14, 1983	45°16.1'S 150°21.4'E	ST	0-150**	Night
2	16, 1983	52°04.2'S 149°43.1'E	SA	0-500	Day
4	23, 1983	64°40.6'S 150°42.6'E	AT/PI	0-500	Day
3-B	25, 1983	61°27.1'S 150°03.9'E	AT	0-750	Day
AC-I-C	28, 1983	56°11.4'S 150°03.6'E	AC	0-750	Day
STC-I-C	Jan. 1, 1984	46°44.7'S 150°05.2'E	STC	0-750	Day
PI-2	16, 1984	64°10.7'S 136°13.7'E	AT/PI	0-750	Day
5	19, 1984	65°02.4'S 118°16.9'E	AT/PI	0-750	Day
6	21, 1984	60°01.2'S 116°04.7'E	AT	0-750	Day
7	26, 1984	44°50.0'S 114°56.0'E	SA	0-750	Day/Night
8	28, 1984	39°54.1'S 114°55.5'E	ST	0-750	Night

\* Pooled five divided sampling layers: 0-50, 50-100, 100-250, 250-500 and 500-750 m.

\*\* 0-50, 50-100 and 100-150 m.

ST: Subtropical, STC: Subtropical Convergence, SA: Subantarctic, AC: Antarctic Convergence, AT: Antarctic, PI: Pack-ice zone.

cated as closer as possible to the original design according to the descriptions by KEMP *et al.* (1929). The sampling data are given in Table 2, *i.e.*, six stations along the 150°E transect, three along the 115°E transect and two others. The sampling with the N70V net was conducted during the daytime except two cases in subtropical stations. The towing procedure also followed the Discovery Investigations. The net was towed vertically at a speed of 1m/s, and plankton were collected from the five layers, namely, 0-50, 50-100, 100-250, 250-500 and 500-750 m. Although 100-750 m net tow was made routinely in the Discovery Investigations, the haul in this layer was not made in the present study. The depth at which the net was closed was different within the distance range of  $\pm 2.3$ -5.9 m from the desired closing depth, and it was also  $\pm 1.8$ -12.4 m for the depth the net reached. That is, the net reached and closed well within an appreciable depth range by the length of wire cable payed out. The closing of the net was made using a closing mechanism while the net was being towed continuously. No flow-meter was mounted on the net. The collected materials were preserved in 10% borax neutralized formalin, and the plankton biomass was expressed in gram wet weight. The biomass was demonstrated in gram wet weight per each 50 m net tow. For example, the biomass in 250-100 m column was reduced to 1/3 to obtain an average zooplankton abundance per 50 meter water column. This method was the same as the one by FOXTON (1956). Unusually large organisms that were occasionally collected

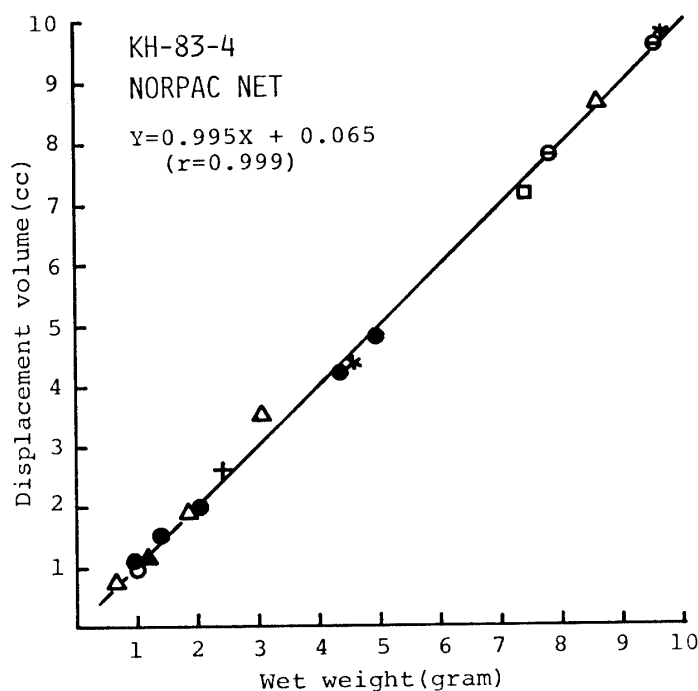


Fig. 1. Relationship between displacement volume and wet weight of zooplankton of different species composition collected with a twin Norpac net (GG 54: 0.33 mm mesh apertures) in the Antarctic. The principal organisms constituting the samples are as follows: Circle: *Chaetognatha* + *Euphausiacea*, Circle with bar: monospecific *Copepoda*, Filled circle: *Chaetognatha* + *Copepoda*, Open triangle: diatoms, Filled triangle: diatoms + *Salpa* spp., Square: *Salpa* spp., Cross: mixed *Copepoda*, Asterisk: sample taken with a XX 13 (0.1 mm mesh apertures) netting.

were removed before measuring the biomass.

Figure 1 shows the volume (ml)–wet weight (g) relationships in macrozooplankton samples of different compositions, which were collected vertically with the twin Norpac net through the 0–150 m layer. A linear relation was observed between two sets of data with a coefficient of correlation approximately 1.0, and this indicates that the wet weight data can be compared directly with the displacement volume data by FOXTON (1956) without correction.

### 3. Results

#### 3.1. Distribution of total zooplankton biomass

The vertical distribution of zooplankton biomass is shown in Fig. 2. Since most of diurnal vertical migration of the Antarctic zooplankton is confined well within the upper 750 m layer (HARDY and GUNTHER, 1935), and zooplankton that migrate to and from the layer deeper than 750 m are very few, the biomass shown in Fig. 2 is considered to give a general abundance of the macrozooplankton in the upper 0–750 m water column. The notable distribution pattern was a concentration of large amounts of zooplankton in the upper 0–100 m, especially in the first 0–50 m, but two stations, Stns.

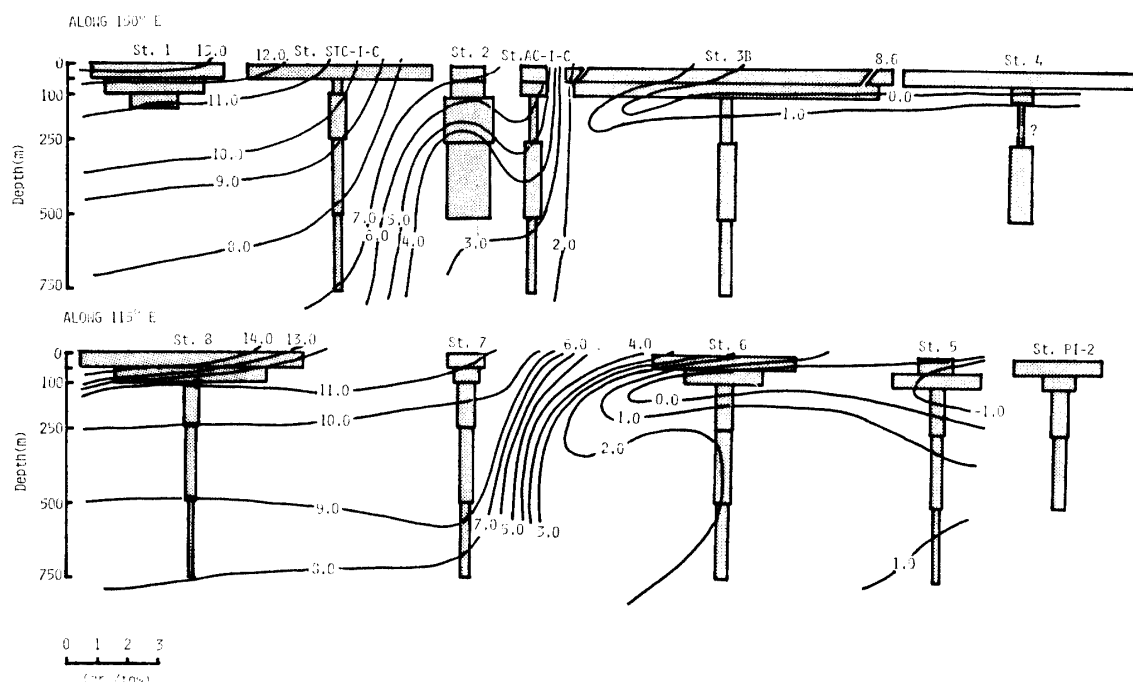


Fig. 2. Vertical distribution of zooplankton collected with a N70V net at the stations along 150°E and 115°E, along with the approximate temperature (°C) profiles (wet weight g/haul).

2 and AC-I-C, showed different patterns from others. At Stn. 2 very small salps, ostracods and chaetognaths predominated in the 500–250–100m layers. In the 500–250m layer at Stn. AC-I-C large sized chaetognath was the responsible organism for the reversed biomass distributions. A similar pattern was also observed at Stn. 7 and all of these three stations were located in the Antarctic Convergence Zone. At the stations from the Subtropical to the Convergence Zone, the principal organisms in the upper 0–100m were composed of gelatinous animals, largely *Doliolum*, salps and pyrosoma. In the southern waters, on the other hand, all stations were located under the influence of the Antarctic Surface Waters in the shallower layers, where an unusually large biomass by the co-existing diatoms was occasionally observed in the surface layer. The Antarctic Surface Waters was characteristic with high concentrations of D. O. (7.5 ml/l),  $\text{PO}_4\text{-P}$  (1.5–2.0  $\mu\text{g/l}$ ) and Silicate-Si (10–60  $\mu\text{g/l}$ ), and low in both salinity and temperature (OCEAN RESEARCH INSTITUTE, UNIV. TOKYO, 1985).

In all the 48 samples collected at 11 stations, Copepoda were most dominant zooplankton component as have been demonstrated elsewhere (HARDY and GUNTHER, 1935; MACKINTOSH, 1937; HOPKINS, 1971). The principal zooplankton taxa next to Copepoda based on the individual numbers were Chaetognatha, Ostracoda and Euphausiacea. In Table 3 the occurrence of each taxon is indicated in terms of the number of samples where they occurred with an individual number of the first five dominance ranks in each sample. The general trends did not differ largely among the sea regions, but there was a gradual increase in the number of dominant taxa towards higher latitudes where the importance of Polychaeta and Coelenterata can be pointed out. Figure 2 was constructed with the same procedure as that by FOXTON (1956). As shown in Fig. 2,

Table 3. Percent frequency of the number of samples containing given zooplankton taxa of first five ranks of dominance to the total number of samples. For sea region see Table 2.

Number of station	2	1	2	1	5
Total number of samples collected	7	5	10	4	22
Sea region	ST	STC	SA	AC***	AT
Chaetognatha	100.0	100.0	100.0	100.0	90.9
Euphausiacea*	57.1	80.0	80.0	75.0	36.4
Ostracoda	85.7	80.0	100.0	100.0	59.1
Salpa spp.	28.6	—	20.0	25.0	13.6
Limacina sp.	14.3	—	10.0	25.0	27.3
Pyrosoma	14.3	—	—	—	—
Polychaeta	28.6	100.0	30.0	25.0	86.4
Coelenterata	57.1	60.0	50.0	50.0	63.6
Doliolum spp.	57.1	40.0	30.0	—	4.5
Appendicularia	57.1	40.0	30.0	25.0	68.2
Amphipoda	—	—	10.0	75.0	4.5
Creseis sp.	—	—	—	—	9.1
Decapoda**	—	—	—	—	9.1
Clio sp.	—	—	—	—	9.1
Euphausiacea (egg)	—	—	40.0	—	—

\* Nauplius, furcilia and calyptopis.

\*\* Larvae.

\*\*\* Lacks 750–500 m haul.

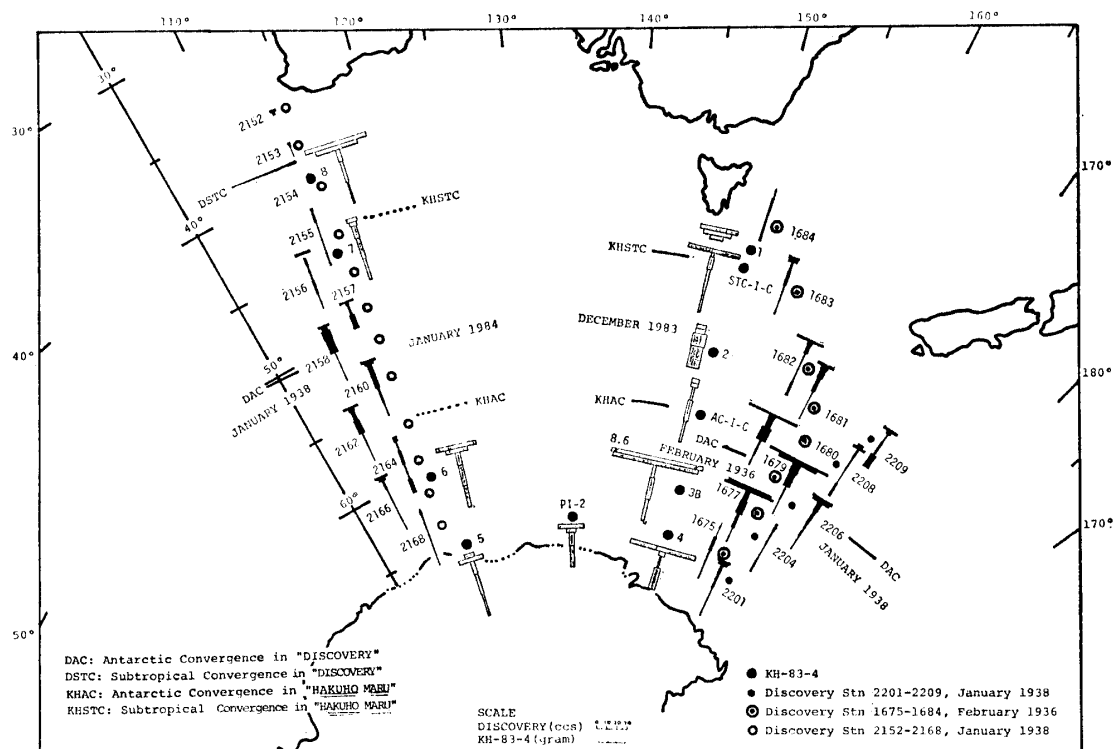


Fig. 3. Comparison of distribution profiles of zooplankton at present (shade) and in the past (filled: FOXTON, 1956). All zooplankton samples in the figure were collected with the N70V net.

the abundance of total zooplankton in the vertical column decreased rapidly with an increase in depth. In Fig. 3 both FOXTON's figures and the result of the present study are demonstrated. Although FOXTON (1956) treated some 2100 samples, most of data were from the Scotia Sea region. Therefore, the data that can be compared with the present study are relatively scarce. Details of the distribution pattern in both data differed from station to station, especially at the Discovery stations located in the south of 60°S where the changes in the depth distribution were less prominent. However, both figures, on the whole, showed quite similar distribution patterns. The average zooplankton biomass obtained in the present study is given in Table 4, and that by FOXTON (1956) in the Discovery Investigations is given in Table 5. It is observed in both tables that the biomass in the 0–50 m and 50–100 m layers in the present study is larger than in FOXTON's data, especially for the Subtropical and Subantarctic regions. Table 6 shows the comparison of the whole zooplankton biomass at present and in the past. Since the plankton abundances in the upper 0–100 m showed local variations by the

Table 4. Average zooplankton biomass of fifty net samples collected in different areas of Subantarctic and Antarctic water masses (g wet weight per haul).

Sea region Station	ST 1, 8	STC STC-I-C	SA 2, 7	AC AC-I-C	AT 3B, 6	PI 4, 5, PI-2
0–50	5.93**	6.10	1.18	0.85	10.92*	3.96*
50–100	4.06**	0.37	0.98	0.85	6.37*	1.59*
100–250	1.09	1.70	3.22	0.66	1.21	0.79
250–500	1.58	1.05	4.29	2.84	1.42	2.50
500–750	0.78	1.04	1.37	1.43	1.83	1.19

\* Contaminated by diatoms.

\*\* Contaminated by doliolids.

Table 5. Average zooplankton biomass in the Discovery Investigations† (displacement volume per haul in c.c.).

Sea region No. of station included	I			II		III	
	ST	SA	AT	SA	AT	SA	AT
	2	4	6	2	3	5	3
0–50	0.50	0.95	1.08	1.15	1.85*	2.20**	3.70
50–100	0.25	0.23	0.67	1.00	1.45*	0.83**	3.23
100–250	0.40	0.90	1.40	0.75	1.33	1.40	1.73
250–500	—	1.28	2.57	1.25	1.57	2.46	3.33
500–750	—	0.95	0.78	2.00	0.93	1.16	1.33

† Constructed from FOXTON (1956, Table 11d).

\* Sample rich in phytoplankton.

\*\* Excluded 1 sample composed entirely of salps (salps in FOXTON's table).

I: 35°15.3'S–63°29.1'S, 114°45.0'E–115°52.1'E, 30 XII 1938–10 I 1939, 12 stations out of Stns. 2152–2168.

II: 53°07.7'S–65°48.1'S, 162°17.6'E–168°56.4'E, 22–27 I 1939, Stns. 2201, 04, 05, 08 and 2209.

III: 43°45.5'S–64°29.5'S, 152°00.5'E–163°00.8'E, 5–14 II 1936, 8 stations between Stns. 1675–1684.

Table 6. Average zooplankton biomass pooled for 0-750 and 100-750 m water columns.

Sea region	Subantarctic		Antarctic	
	0-750	100-750	0-750	100-750
Water column (m)				
Present study	11.04	8.88 (4.37)*	15.89	4.47
FOXTON (1956)**	6.17	4.05	8.98	4.99

\* Biomass excluding unusually large value at Stn. 2 is given in parentheses.

\*\* Combined and averaged columns I, II and III in Table 5.

contaminated diatoms and others, comparison of biomass in the layers below 100 m is considered to give more reasonable figures. A slightly larger biomass was found in the present study for both the Subantarctic and Antarctic waters. Although no statistical test was made because of insufficient data in the present study, these two data sets, the biomass in the KH-83-4 and the Discovery Investigations, showed only  $\pm 8-11\%$  difference from each other. As will be discussed later, the comparison indicated that there were no notable differences in the total macrozooplankton biomass at present and in the past.

### 3.2. Abundances of major herbivorous copepod species

It is considered that an increase of enormous amount of surplus krill during the past 50-60 years perhaps caused some changes in the feeding conditions among many other herbivorous zooplankters that may share the same and/or similar forage with *E. superba*. Among these herbivores, copepods might have been largely affected with such environmental changes so as to decrease their population size. It is, therefore, worth to examine whether or not possible changes in copepod community are observed. In Table 7 the abundances of major copepod species are shown in terms of the pooled individual numbers through the sampling column. Both *Rhincalanus nastus* and *Calanus tonsus* are the Subtropical to Subantarctic species. Since the comparable data on the abundance of copepod species in the Discovery Investigations were limited,

Table 7. Pooled number of individuals of copepods collected with the duplicated N70V net in the Pacific to Indian Ocean sectors of the Antarctic during the HAKUHO MARU cruise KH-83-4 (BIOMASS SIBEX I).

Sea region	Subtropical STC			Subantarctic		AC	Antarctic		Pack-ice		
Station	1	8	STC-I-C	2	7	AC-I-C	3B	6	4	5	PI-2
Date	Dec. 14	Jan. 28	Jan. 1	Dec. 16	Jan. 26	Dec. 28	Dec. 25	Jan. 21	Dec. 23	Jan. 19	Jan. 16
Water column (m)	150-0	750-0	750-0	500-0	750-0	750-0	750-0	750-0	500-0	750-0	500-0
<i>Rhincalanus nastus</i>	4			701	1						
<i>Rhincalanus gigas</i>						272	30	279	86	23	75
<i>Calanoides acutus</i>				25		24	304	915	74	236	186
<i>Calanus simillimus</i>	20	42	120	1002	253	268	43	6	5		7
<i>Calanus propinquus</i>						7		13		33	6
<i>Eucalanus</i> spp.*	28	9	5	13	57	107					
<i>Calanus tonsus</i>	121	6									

\* *E. elongatus* + *E. longiceps*



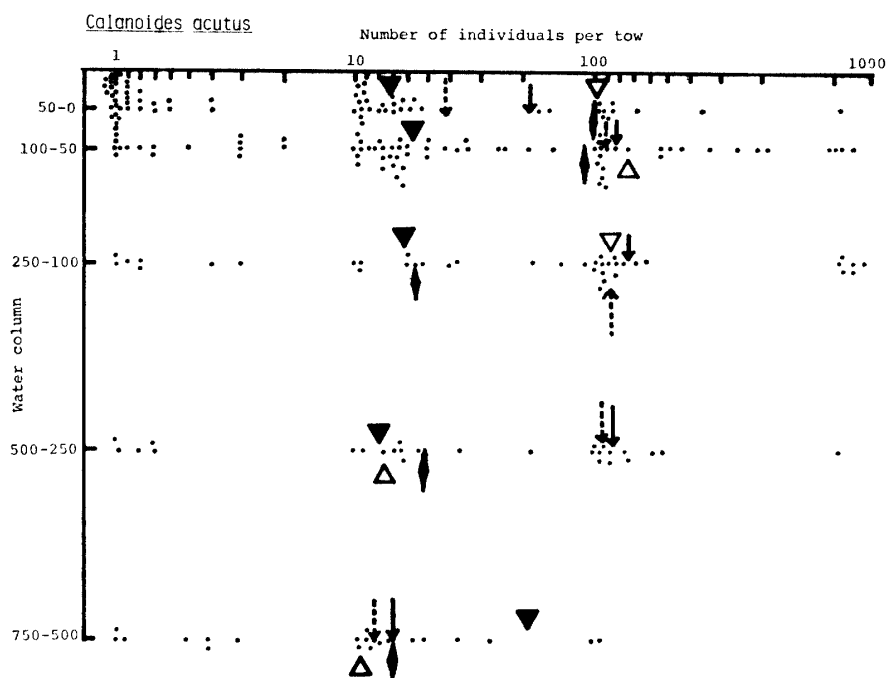


Fig. 4. Vertical distribution of *Calanoides acutus*. Plots represent abundance of the species in five layers of the present study and all *Discovery*'s data which are seasonally comparable with the present result. Averages for; ← South Georgia, December–January, 1926–1927 (HARDY and GUNTHER, 1935), ←--- South Georgia, November–March, 1926–1927 (HARDY and GUNTHER, 1935), △ Drake Passage (80° W), November–December, 1933–1934 (MACKINTOSH, 1937), ▲ Indo-Pacific, December–January, 1983–1984 (present study), ◆ Whole antarctic, December–January, 1925–1939, 1950–1951 (ANDREWS, 1966).

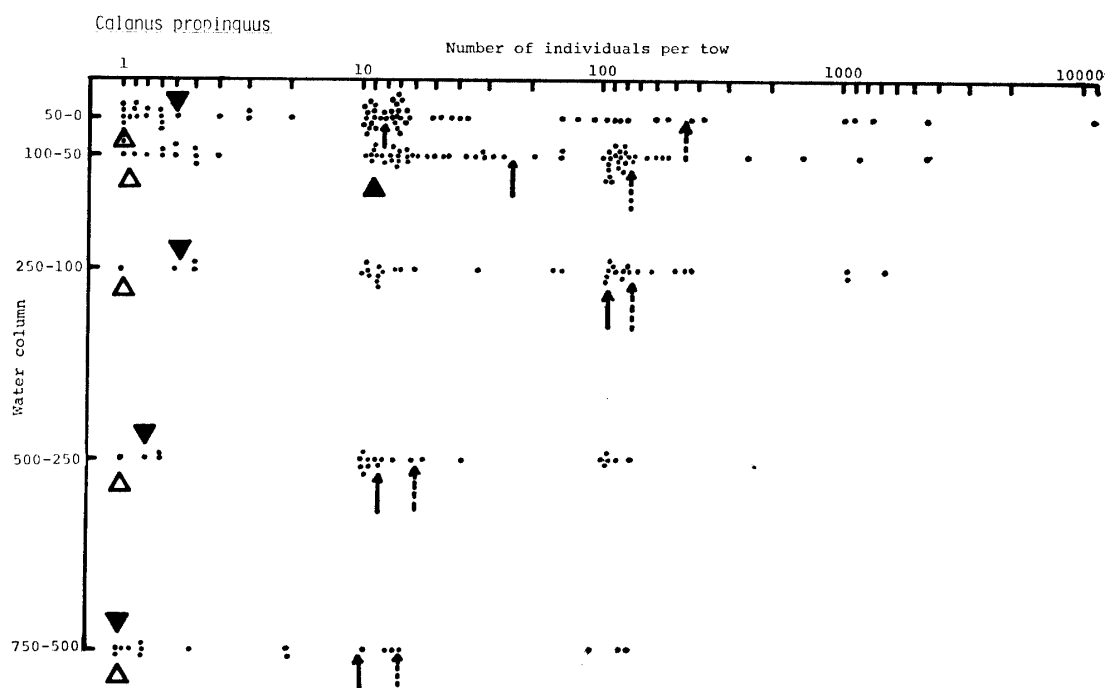


Fig. 5. Same as Fig. 4 but for *Calanus propinquus*.

four representative Antarctic species were selected; *Calanus propinquus*, *C. simillimus*, *Calanoides acutus* and *Rhincalanus gigas*. Among the four species, *C. propinquus* alone showed an unusually small number of individuals, but on the whole no unusual or different distribution pattern was observed in comparison with that known in this sea

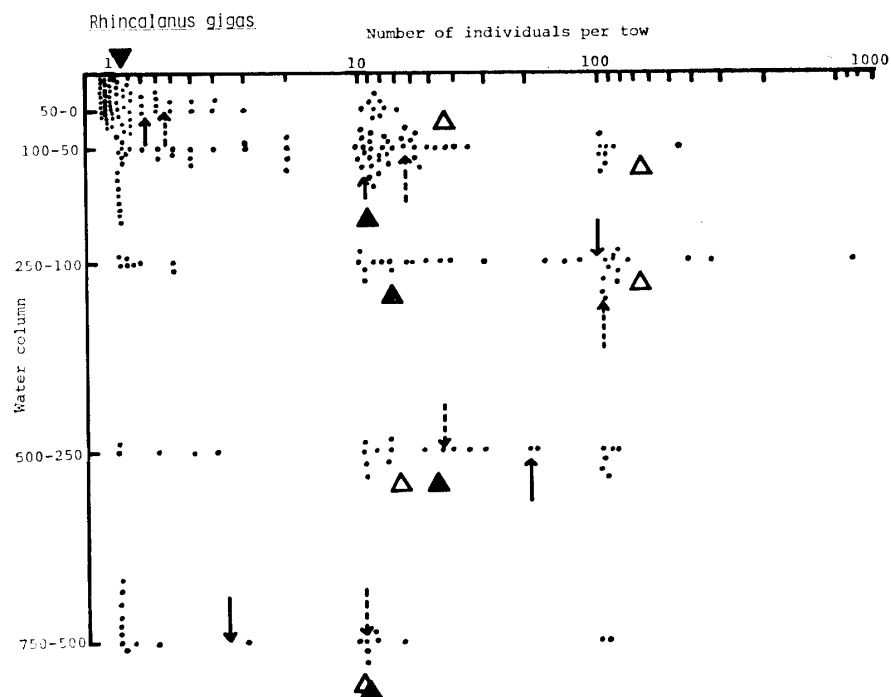


Fig. 6. Same as Fig. 4 but for *Rhincalanus gigas*.

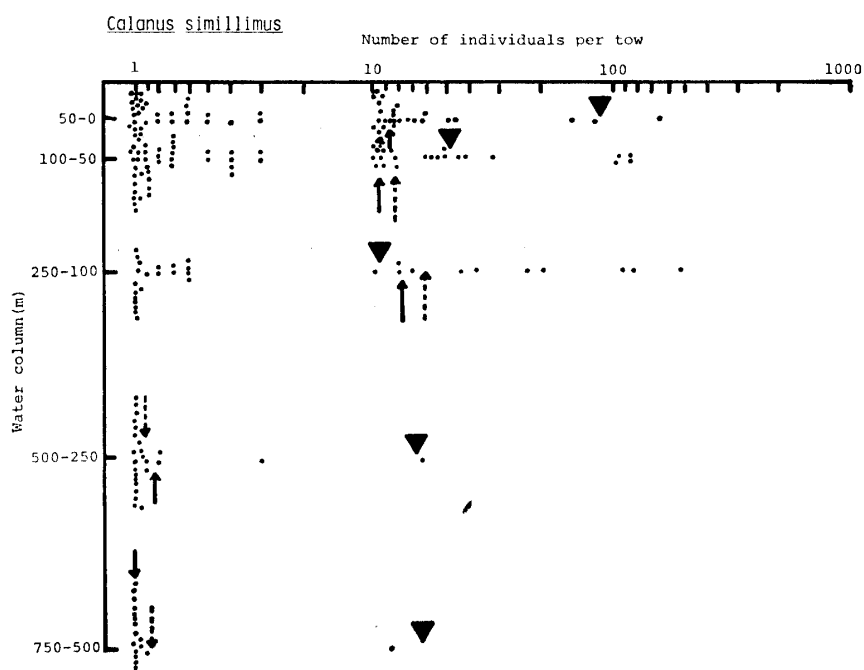


Fig. 7. Same as Fig. 4 but for *Calanus simillimus*.

region (e.g. BRODSKII, 1966).

In comparing the abundances of four copepod species, the comparable past data available in the Discovery Reports were those of HARDY and GUNTHER (1935), MACKINTOSH (1937) and ANDREWS (1966). However, there were no data that completely coincided with the present data on the point of sampling locality. Even so, the circumpolar distribution of the Antarctic copepods shows continuous and very slight local variations as a whole (BAKER, 1954) so that the Discovery's data can be compared with the present data. The individual numbers of four major copepod species from all available data are plotted against the depth and shown in Figs. 4–7, and the data are given in appended tables. The abundance of each copepod species varied with sampling seasons, locations and the sampling layers. For example, *C. acutus* in HARDY and GUNTHER's data increased in February to March, in November according to MACKINTOSH's data, whereas such changes were less prominent in ANDREWS' data (1966). A similar variation is also observed throughout the three other species. In the Antarctic the mean total volume of zooplankton in the 0–1000m layers shows a considerable variation with season (FOXTON, 1956). So, it is reasonable to compare the average zooplankton abundances for December to January when the plankton sampling in the present study was conducted, but November to December in MACKINTOSH (1937). As indicated also in the appended tables the number of three copepod species, *R. gigas*, *C. propinquus* and *C. acutus*, in the present study showed the smallest average number of individuals among the data of Discovery Investigations, varying with species and depth of layers (Table 8). A noted difference can be observed with the magnitudes of approximately 1/10 to 1/100 in more than 70% of figures compared. Although there were only one series of previous data for *C. simillimus*, this species alone showed larger individual numbers than the data by HARDY and GUNTHER (1935). The reason is not clarified as yet.

Table 8. Comparison of individual number of four principal copepod species collected with the N70V net at present and in the past (individuals per haul).

Water column (m)	<i>C. acutus</i>				<i>C. propinquus</i>			<i>C. simillimus</i>		<i>R. gigas</i>		
	HG	M	A*	K	HG	M	K	HG	K	HG	M	K
50–0	90.8	123.5	117.5	38.8	28.1	0.0	5.0	23.3	98.8	3.2	66.3	1.7
100–50	266.6	399.3	99.5	53.9	86.4	1.3	19.0	15.7	61.3	19.8	427.5	18.3
250–100	371.7	374.6	56.5	48.9	136.7	0.8	5.3	33.7	14.9	114.9	415.0	35.3
500–250	255.5	37.7	64.5	33.4	27.3	0.0	3.0	2.6	41.6	90.3	41.1	64.0
750–500	41.5	18.6	41.5	91.5	10.1	0.0	1.0	0.0	45.6	7.4	10.3	12.3
Total (750–0)	1026.1	953.2	379.5	266.5	288.6	2.1	33.3	75.3	262.2	235.6	960.2	131.6

HG: HARDY and GUNTHER (1935), Dec. 1926–Jan. 1927.

M: MACKINTOSH (1937), Nov. 1933–Dec. 1934.

A: ANDREWS (1966), Dec. 1925–1939 and Jan. 1950–1951.

K: KAWAMURA—Present study, Dec. 1983–Jan. 1984.

\*: Pooled number of copepodites CIV, CV and CVI.

#### 4. Discussion

The comparison of macrozooplankton abundances between the present study and the Discovery Investigations suggested that the biomass of macrozooplankton at present remained within about  $\pm 10\%$  variations of FOXTON's data for the Subantarctic and Antarctic Zones (see Table 6). The converted biomass from wet weight/haul to dry weight/m<sup>2</sup> at five stations for the Antarctic Zone in the present study were 4.11 g dry wt/m<sup>2</sup>/750–0 m (Table 9), which may indicate a possible but slight increase in the total biomass of the Antarctic macrozooplankton. If so, an increase of salps that show the fastest growth rate among multicellular animals (HERON, 1972) is feasible, and the role of *Salpa thompsoni* must be important for its rapid response to the change in food availability (FOXTON, 1966), but this needs to be confirmed with further samplings.

On the other hand, some major herbivorous copepods such as *Calanoides acutus*, *Calanus propinquus* and *Rhincalanus gigas* were remarkably poor in abundances, although *Calanus simillimus* was more abundant than in the previous data. *C. simillimus* is distributed widely over the Antarctic Ocean, but its pronounced irregular distribution pattern in the circumpolar continuity makes this species different from others. According to BAKER (1954), *C. simillimus* exceeds 50% in the 'frequency of the occurrence' in the waters between 18–140°E, the region close to the present study area, whereas it was about 10% in the South Georgian waters. *C. simillimus* is also known to form dense surface swarms (KAWAMURA, 1974). These distribution characteristics will make the abundance estimation of this species by net sampling to be an erratic. It is, therefore, unable to state whether or not *C. simillimus* actually became more abundant in the recent decades than in the days of the Discovery Investigations. In contrast to this, the average abundances of three other copepod species were remarkably poorer than those of the previous data with a magnitudes of about 1/10 to 1/100 folds as seen in Figs. 4–7. The abundance of zooplankton in quantitative sampling sometimes varies up to 300% (CUSHING, 1962), but the total biomass actually found in this study did not differ largely from the Discovery's data. On the other hand, the very poor abundance in *R. gigas*, *C. propinquus* and *C. acutus* is extraordinary from generally recognized coefficient of variation in zooplankton sampling. Perhaps the above-mentioned three

Table 9. Average biomass of macrozooplankton in the vertical column of 0–1000 m and 0–750 m in the Antarctic Ocean. Wet weight biomass in the present study was converted into dry weight by multiplying 0.1 after HOPKINS (1971) (dry weight g per square meter).

Source of data	HOPKINS (1971)*			KAWAMURA** (Present study) 750–0(m)
	1000–0(m)	1000–0(m)		
Water column				
Sea region	Pacific Sector	Pacific Sector	All Sector	Pacific/Indian Sector
Origin of data	HOPKINS (1971)	FOXTON (1956)		Present study
Subantarctic	2.58	2.10	2.05	2.87
Antarctic	2.67	1.80	2.52	4.11
Antarctic Convergence	—	—	—	1.74

\* Average of all seasons.

\*\* December/January.

copepod species decreased in their population sizes. That is, some changes must have taken place in the species composition of the Antarctic macrozooplankton community, probably induced by the long-term distortions in the interactions of herbivorous planktonic animals, especially between *Euphausia superba* and major herbivorous copepods.

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## Appendix 1

*Average number of individuals in Calanoides acutus collected with the N70V closing net.*

HARDY and GUNTHER (1935)											
Water column (m)	1926 Nov.	1926 Dec.	1927 Jan.	1926/27 Feb.		1926 Mar.		Nov.-Mar. (pooled)		Dec.-Jan. (pooled)	
50-0	28.3(4)	26.8(26)	154.8(17)	101.2(9)		29.2(17)		68.1		90.8	
100-50	91.3(4)	245.5(26)	287.6(17)	123.1(9)		133.6(17)		176.2		266.6	
250-100	141.7(3)	394.5(15)*	348.9(8)**	263.8(8)		1308.0(5)***		232.5		371.7	
500-250	58.7(3)	170.8(10)	340.2(5)	113.9(7)		180.5(2)		172.8		255.5	
750-500	18.5(2)	26.6(9)	56.3(4)	35.8(5)		0.0(1)		27.4		41.5	
MACKINTOSH (1937)											
Water column (m)	ANDREWS (1966)****										Present study
	1934 Nov.	1933 Dec.	Nov.-Dec. (pooled)	1925-1939		1950-1951		Nov.-Mar. (pooled)	Dec.-Jan. (pooled)	Dec.-Jan.	
				Nov.	Dec.	Jan.	Feb.	Mar.			
50-0	205.0(5)	42.0(10)	123.5	61	75	160	183	156	127.0	117.5	38.8(8)
100-50	656.0(5)	142.5(10)	399.3	142	96	103	50	87	95.6	99.5	53.9(8)
250-100	692.0(5)	56.2(10)	374.1	107	58	55	113	67	80.0	56.5	48.9(8)
500-250	31.4(5)	43.9(10)	37.7	83	52	77	127	139	95.6	64.5	33.4(8)
750-500	13.6(5)	23.5(10)	18.6	75	36	47	103	160	84.2	41.5	91.5(4)

\* (230-232)-100 m tows are included (3 tows).

\*\* 224-100 m tow is included.

\*\*\* 230-100 m tow is included.

\*\*\*\* Number of stations examined from November through March was 555, 412, 704, 590 and 492, respectively, in order of month.

*Average number of individuals in Calanus propinquus collected with the N70V closing net.*

Water column (m)	HARDY and GUNTHER (1935)				
	1926 Nov.	1926 Dec.	1927 Jan.	1926/27 Feb.	1926 Mar.
50-0	5.3(4)	32.5(30)	23.6(17)	3104.5(11)	86.0(17)
100-50	5.7(3)	83.7(27)	89.1(17)	1196.5(10)	190.9(17)
250-100	10.3(3)	167.4(12)*	105.9(8)***	870.9(9)	567.2(5)****
500-250	1.3(3)	31.9(10)	22.6(5)	97.4(8)	98.5(2)
750-500	0.0(2)	16.2(9)**	4.0(4)	145.0(5)	—

Water column (m)	HARDY and GUNTHER			MACKINTOSH (1937)			Present study
	Nov.-Mar. (pooled)	Dec.-Jan. (pooled)	1934 Nov.	1933 Dec.	1934 Mar.	Nov.-Dec. (pooled)	
50-0	650.4	28.1	0.0(5)	0.0(10)	0.0(9)	0.0	5.0(2)
100-50	313.2	86.4	2.0(5)	0.5(10)	0.1(9)	1.3	19.0(1)
250-100	344.3	136.7	0.6(5)	0.9(10)	0.1(9)	0.8	5.3(3)
500-250	50.3	27.3	0.0(5)	0.0(10)	1.4(9)	0.0	3.0(4)
750-500	41.3	10.1	0.0(5)	0.0(10)	0.0(9)	0.0	1.0(2)

\* (230-270)-100 m tows are included (3 tows).

\*\* 700-500 m tows are included.

\*\*\* (224-225)-100 m tows are included (3 tows).

\*\*\*\* 230-100 m tows are included.

*Average number of individuals in Calanus simillimus collected with the N70V closing net.*

Water column (m)	HARDY and GUNTHER (1935)							Present study Dec.-Jan.
	1926 Nov.	1926 Dec.	1927 Jan.	1926/27 Feb.	1926 Mar.	Nov.-Mar. (pooled)	Dec.-Jan. (pooled)	
50-0	35.2(5)	37.9(28)	8.6(15)	7.9(7)	3.0(11)	18.5	23.3	98.8(11)
100-50	1018(4)	22.5(27)	8.9(15)	74.4(7)	19.1(11)	28.3	15.7	61.3 (7)
250-100	20.0(3)	20.6(15)*	46.7 (6)	95.1(7)	64.3(3)**	49.3	33.7	14.9 (8)
500-250	1.7(3)	5.1(10)	0.0 (3)	1.9(7)	0.0(1)	1.7	2.6	41.6 (9)
750-500	10.5(2)	0.0 (8)	0.0 (2)	1.0(4)	0.0(1)	2.3	0.0	45.6 (5)

\* (225-232)-100 m tows are included (5 tows).

\*\* 230-100 m is included.

*Average number of individuals in Rhincalanus gigas collected with the N70V closing net.*

Water column (m)	HARDY and GUNTHER (1935)					Present study Dec.-Jan.
	1926 Nov.	1926 Dec.	1926/27 Jan.	1926/27 Feb.	1926 Mar.	
50-0	2.8(5)	1.8(29)	4.6(17)	7.6(9)	6.8(17)	
100-50	47.8(4)	25.6(28)	13.9(17)	73.2(9)	83.8(17)	
250-100	82.7(3)	137.5(15)*	9.3(8)**	220.4(8)	257.8 (5)	
500-250	18.3(3)	58.6(10)	122.0(5)	78.0(7)	47.0 (2)	
750-500	0.5(2)	7.5 (8)	7.3(4)	59.6(5)	0.0 (1)	

Water column (m)	HARDY and GUNTHER		MACKINTOSH (1937)			Present study Dec.-Jan.
	Nov.-Mar. (pooled)	Dec.-Jan. (pooled)	1934 Nov.	1933 Dec.	Nov.-Dec. (pooled)	
50-0	4.7	3.2	52.0(5)	80.5(10)	66.3	1.7(6)
100-50	48.9	19.8	265.0(5)	590.0(10)	427.5	18.3(6)
250-100	141.5	114.9	608.8(5)	221.2(10)	415.0	35.3(6)
500-250	64.8	90.3	50.6(5)	31.6(10)	41.1	64.0(6)
750-500	15.0	7.4	3.4(5)	17.2(10)	10.3	12.3(4)

\* (224-230)-100 m tows are included (5 tows).

\*\* (224-225)-100 m tows are included (3 tows).